

**IDEA AND  
PERSPECTIVE****The myth of plant species saturation**

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**Abstract**

Plant species assemblages, communities or regional floras might be termed ‘saturated’ when additional immigrant species are unsuccessful at establishing due to competitive exclusion or other inter-specific interactions, or when the immigration of species is off-set by extirpation of species. This is clearly not the case for state, regional or national floras in the USA where colonization (i.e. invasion by exotic species) exceeds extirpation by roughly a 24 to 1 margin. We report an alarming temporal trend in plant invasions in the Pacific Northwest over the past 100 years whereby counties highest in native species richness appear increasingly invaded over time. Despite the possibility of some increased awareness and reporting of native and exotic plant species in recent decades, historical records show a significant, consistent long-term increase in exotic species (number and frequency) at county, state and regional scales in the Pacific Northwest. Here, as in other regions of the country, colonization rates by exotic species are high and extirpation rates are negligible. The rates of species accumulation in space in multi-scale vegetation plots may provide some clues to the mechanisms of the invasion process from local to national scales.

**Keywords**

Biotic resistance, competitive exclusion, habitat heterogeneity, invasion, plant diversity, saturation, species richness.

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**INTRODUCTION**

There is a continuing scientific debate on whether plant communities or regions can become ‘saturated’ with species (Hillebrand 2005; Freestone & Harrison 2006). The current paradigm based on theories of competitive exclusion (Grime 1973) and biotic resistance (Elton 1958) suggest that species-rich areas are less prone to colonization because different species have different resource requirements (Tilman 2004), and because resources such as light, water, nutrients, and warm temperatures are usually limited in terrestrial systems resulting in the exclusion of newly arriving propagules (Rejmánek 1996; Loreau 2000). That available niches might be full (sensu Tilman 1999) continues to be used to argue that diverse communities are resistant to invasion. In fact, as recently as 2002, some ecologists claimed that ‘...diverse communities will probably require minimal maintenance and monitoring because they are generally effective at excluding undesirable invaders’ (Kennedy *et al.* 2002).

However, it is likely that niche availability changes in space and time because most terrestrial ecosystems are subjected to disturbances and other ‘space-creating’ pro-

cesses (e.g. fire, flooding, grazing, insect outbreaks and plant death). Such mechanisms, at least theoretically, provide ample opportunities for external propagules to become established in plant communities.

The invasion of species over time from outside the community, region or country adds an interesting component to our understanding of saturation (Rejmánek 1996; Lonsdale 1999; Mack *et al.* 2000; Pyšek & Hulme 2005). Continued species invasions led us to pursue the present study. That is, the invasion of exotic plant species offer us the opportunity to evaluate some important aspects of local (plot-level) and regional (county, multi-county) saturation of plant species in the US. It is noteworthy that even some of the smallest US counties show little or no indication of plant species saturation. Consider, for example, Philadelphia County, an area of 350 km<sup>2</sup> in southeastern Pennsylvania, one of the smallest counties, having 2035 species (making it the most floristically diverse county within the eastern US), of which a full 26% or 705 species are exotic species. Other small counties located within large metropolitan areas, such as Bronx County, NY, New York County, NY, Newport County, RI and Fairfax County, VA, show similar yet less

dramatic patterns in increased species numbers due to exotic introductions, but without evidence of native species extirpation at the count-level (Kartesz 2007). How important can competitive exclusion and biotic resistance be if exotic species can easily invade even small counties? Is species saturation a myth?

We reviewed the current literature and took a fresh look at existing datasets to better understand issues related to saturation of plant species assemblages within regional and national floras with respect to modern plant species invasions. We begin by examining colonization and extirpation rates.

### COLONIZATION (INVASION) AND EXTIRPATION

The best currently available data of the vascular flora at the US county-level (<http://www.BONAP.org>) were used to determine the number of naturalized, reproducing species in the conterminous US. Decades of field research coupled with intense herbarium and museum specimen assessment from collections throughout North America, critical review and assessment of vast quantities of published and unpublished monographs and revisions, and floristic county-level summaries of vascular plants were incorporated into BONAP to make the county-level datasets as comprehensive as possible. At the county scale, a species was determined to be exotic (or non-native) if it was not native to the county. State, region and national-scale determinations were made in a similar way.

For documented plant extinctions and extirpations in the USA, we relied on data from NatureServe (Jason McNeese, personal communication, 9 May 2007). Counts were for vascular plants only at the species level (no sub-species or varieties). Native species included extant and extirpated species. Exotic species included those that were introduced non-native aliens into the geographical area of interest (e.g. conterminous US, multi-state region, or state). Possibly extirpated species included those that are *presumed* (species believed to be extirpated from the nation or state despite intensive searches of historical sites and other appropriate habitat, and little chance for rediscovery) or *possibly* (species that occurred historically in the nation or state, its occurrence has not been verified in the past 20–40 years, but there is some possibility of rediscovery) *extirpated* from the species pool as determined by NatureServe (<http://www.natureserve.org/explorer/ranking.htm>).

The number of naturalized, reproducing species greatly exceeds the number of documented plant extirpations in the conterminous US and in all the subregions where data were immediately available (Table 1). Thus, after the first 400 years since European settlement, there has been about a 17.9% increase in the conterminous flora with only a 0.6% extirpation rate (Table 1). On the Hawaiian Islands, where extinction is predicted to be equitable to invasion under

**Table 1** Estimates of native, colonized exotic species, and extirpations in the vascular plants of northwestern states, Hawaii, and the conterminous US\*

Area	Native taxa†	Colonized exotic taxa	Possibly extirpated natives	Ratio colonization to extirpation
Washington	2527	562	17	33 to 1
Oregon	3215	669	33	20 to 1
Idaho	2485	377	10	38 to 1
Montana	2240	411	19	22 to 1
Wyoming	2316	363	35	10 to 1
PNW (five states above)	4655	913	35	26 to 1
Hawaii	1259	1058	90	12 to 1
Conterminous US (species)	15630	3021	105	29 to 1
Conterminous US (species)‡	15233	3363	140	24 to 1

\*Source for all data except the last row: NatureServe (Jason McNeese, personal communication, 9 May 2007; <http://www.natureserve.org/explorer/>).

†Includes the count of species for which origin is currently undetermined. The vast majority of these 'origin unknown' species are expected to be classified as native.

‡Source: Biota of North American Program, <http://www.BONAP.org>. Count includes species, subspecies or varieties.

equilibrium conditions (MacArthur & Wilson 1963), colonization still exceeds extirpation of plant species by almost a 12 to 1 margin (Table 1, see data for Hawaiian Islands). There may be a lag effect in extirpation or extinction, but the overall pattern is one of apparent species coexistence (or biotic acceptance; Stohlgren *et al.* 2006b) rather than one of saturation, competitive exclusion or biotic resistance at these spatial scales (Table 1).

This is not to say that there have not been decreases in abundance of many native plant species. However, we could not find any evidence of significant reductions in native species abundance attributed to the establishment of non-native plant species, leading to reported extirpations or extinctions. Except for Hawaii, non-native plant species continue to make up < 20% of regional floras (Table 1). Direct habitat destruction (e.g. land use conversion for agriculture and urban development) and invasive pathogens (e.g. Dutch elm disease, chestnut blight) have been noted as proximate causes of native plant species declines.

### REGIONAL TEMPORAL TRENDS IN COLONIZATION BY EXOTIC PLANT SPECIES

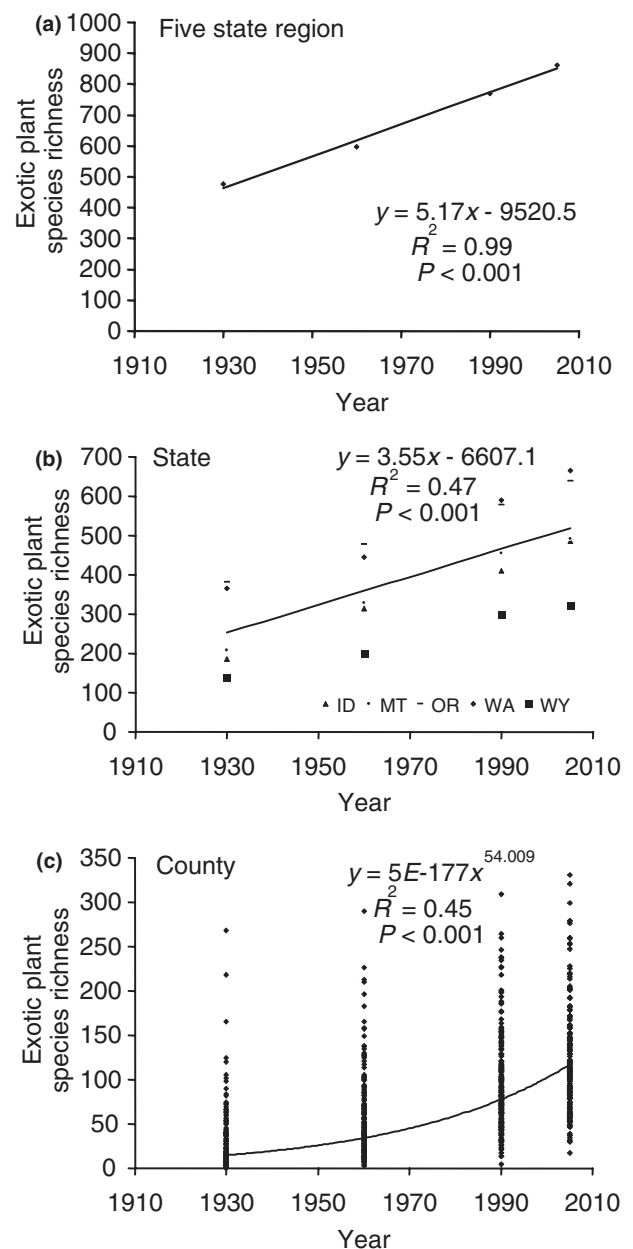
The data necessary to investigate regional temporal trends of invasion are not uniformly available across the US. Data on temporal trends of invasion were available in the Pacific

Northwest (INVADERS Database, Dr Peter Rice, <http://invader.dbs.umt.edu/>, covering Washington, Oregon, Idaho, Montana, and Wyoming. We compiled new records of exotic plant species in convenient time periods (1900–1930; 1931–1960; 1961–1990; 1991–2005) for three spatial scales: sub-region (county), small region (state) and large region (five-state area).

Regional temporal trends of invasion in the Pacific Northwest demonstrate continued colonization, increased reporting completeness or both (Palmer 2005). For the time periods and spatial scales examined, there were significant increases in exotic species richness over time (Fig. 1a–c). At the county scale (Fig. 1c), the relationship fit an increasing power model.

There are always caveats associated with observation data of this type related to differences in reporting effort or survey completeness over time. We acknowledge that botanical surveys may have improved over time for native and exotic species, but we have no evidence of reporting bias for either group. Statewide and regional numbers of native plant species have been relatively stable over the past 20 years (J. Kartesz, personal communication). There has been increased awareness of rare native and harmful invasive species. However, the obvious recent spreading of several showy species such as yellow sweet clover (*Melilotus officinalis*), leafy spurge (*Euphorbia esula*), and purple loosestrife (*Lythrum salicaria*) over the five-state area produce strikingly similar patterns compared to reports from well-surveyed counties with > 50 exotic species (Fig. 2). Likewise, with increased trade, transportation and land use change and disturbance, exotic species likely have continued to invade and spread. However, our best judgment is that the patterns of invasion reflect the actual invasion process rather than sampling deficiencies in the past (Fig. 2). There is growing support that at various scales, these increases in exotic species over time are not artefacts of sampling efficiency, but reality (Pyšek *et al.* 2003; Palmer 2006).

The most striking trend in invasion was the very consistent steepening of the relationship between native and exotic plant species densities over time (Fig. 3). By 1930, there was already a highly significant, positive, non-linear relationship between the density of native and non-native plant species in a county, with 53% of the variation in non-native species density explained by native species density. Over time the rate at which non-native species increased with the density of native species has generally increased. The 2005 time period is only half as long (15 years compared to 30 years) as the other time periods, and it is not unreasonable to expect the relationship and model coefficients to increase in the next 15 years. In short, the most species-rich counties continued to be invaded at faster rates than species-poor counties over time. Even in the face of an ever growing number of established non-

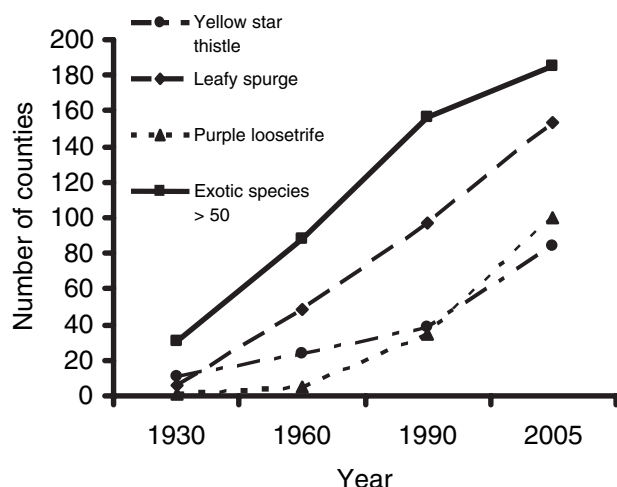


**Figure 1** Exotic species richness over specific time periods (1900–1930; 1931–1960; 1961–1990; 1991–2005) for three spatial scales in Pacific Northwest states (Washington, Oregon, Idaho, Montana and Wyoming); by the five-state region (a), by state (b); and by county (c).

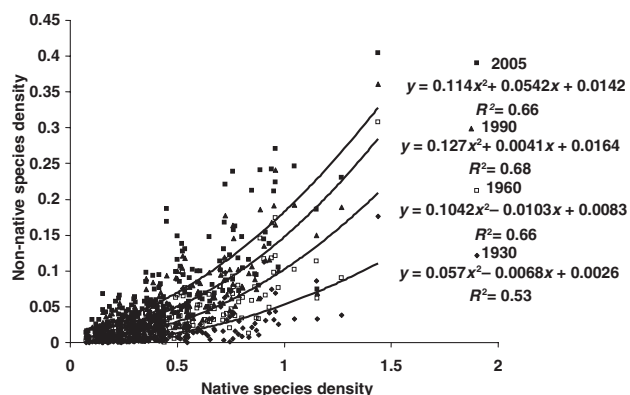
native species, there is little evidence that species membership is being constrained (Table 1, Figs 1–3).

## COLONIZATION (INVASION) OF LOCAL PLANT ASSEMBLAGES

How complete or incomplete is the invasion to date? What types of plant assemblages are these immigrants invading



**Figure 2** Reported increases in the number of counties with > 50 exotic species and the number of counties reporting yellow sweet clover (*Melilotus officinalis*), leafy spurge (*Euphorbia esula*), and purple loosestrife (*Lythrum salicaria*) over the same five-state area as in Fig. 1.



**Figure 3** The relationship between native and exotic plant species densities over time in counties in the Pacific Northwest states (Washington, Oregon, Idaho, Montana and Wyoming). Simple species densities were used (i.e. number of species divided by county area) to adjust for differences in county areas (see Stohlgren *et al.* 2005a; Flather *et al.* 2006).

within species-rich and species-poor counties, states and regions? We know some plant communities have been more heavily invaded than others (Stohlgren *et al.* 2006b), and only long-term careful monitoring could prove whether rates of invasion or local richness are increasing. We know that at county and state scales in the continental US (Stohlgren *et al.* 2005a) and floras throughout the world (Lonsdale 1999; Richardson *et al.* 2005), we often see positive relationships between native and exotic species richness, respectively, suggesting that niche space for

**Table 2** Descriptive statistics for native and non-native species richness and cover for 727 plots (0.1 ha) in 36 vegetation types in the central US

	Native species richness	Non-native species richness	Native species cover (%)	Non-native species cover (%)
Minimum	4.0	0.0	0.8	0.0
Maximum	76.0	20.0	172.6	86.9
Mean	27.8	2.3	33.9	5.3
Median	26.0	1.0	28.6	1.8
Standard error	0.5	0.1	1.0	0.4
C.V. (%)	44%	115%	75%	170%

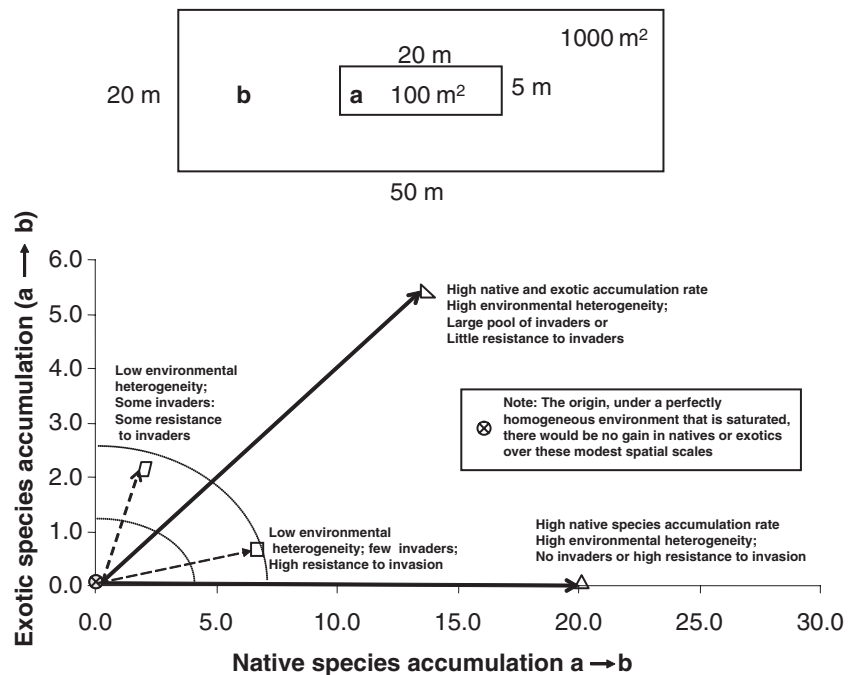
Non-native species were absent in 293 plots.

invading species and resource availability may positively co-vary (Stohlgren *et al.* 2005b, 2006a). But, again, we do not know the rate of invasion in space and time for various plant communities.

We propose that, at least in the US, the spatial patterns of invasion we observe today are the result of the first 400 years or so of plant introduction and spread. Presently, we report a fairly low contribution of non-native plants at plots scales (i.e. low mean and median values for richness and cover; Table 2). The median foliar cover of exotics represents < 6% of total foliar cover at plot scales. The median non-native species represent < 4% of the total species richness at plot scales. The high coefficients of variation further suggest the patchy nature of the current invasion (Table 2). This would likely increase the potential for native species to escape extirpation in space and time, and promote the coexistence (e.g. Huston 1979) of native and non-native species from plot scales to national scales.

We also propose that detailed field studies using multi-scale plots can provide important insights into the patterns of plant invasions that may scale up to county and regional scales. For example, over modest spatial scales between 100 m<sup>2</sup> and 1000 m<sup>2</sup> in a perfectly homogeneous and saturated community, we might expect little or no accumulation of native or exotic species (Fig. 4). Conversely, significant accumulation of native and exotic species over modest spatial scales in a plot in a given community might suggest high environmental heterogeneity, a large regional species pool, or a less-saturated community (Fig. 4).

To investigate the plot-level species assemblages (or communities) and the relationships of native and exotic species richness, we relied on our past landscape-scale studies that used the modified-Whittaker multi-scale sampling design (Stohlgren 2007). Primary study sites included Rocky Mountain National Park, Colorado and the Grand Staircase-Escalante National Monument, Utah with secondary sites scattered across the central US (Stohlgren *et al.*



**Figure 4** Theoretical relationships of native and exotic accumulation of species between (a) 100 m<sup>2</sup> and (b) 1000 m<sup>2</sup> plots for vegetation types with no additional exotic species, some exotic species, and many exotic species colonizing in the larger plot.

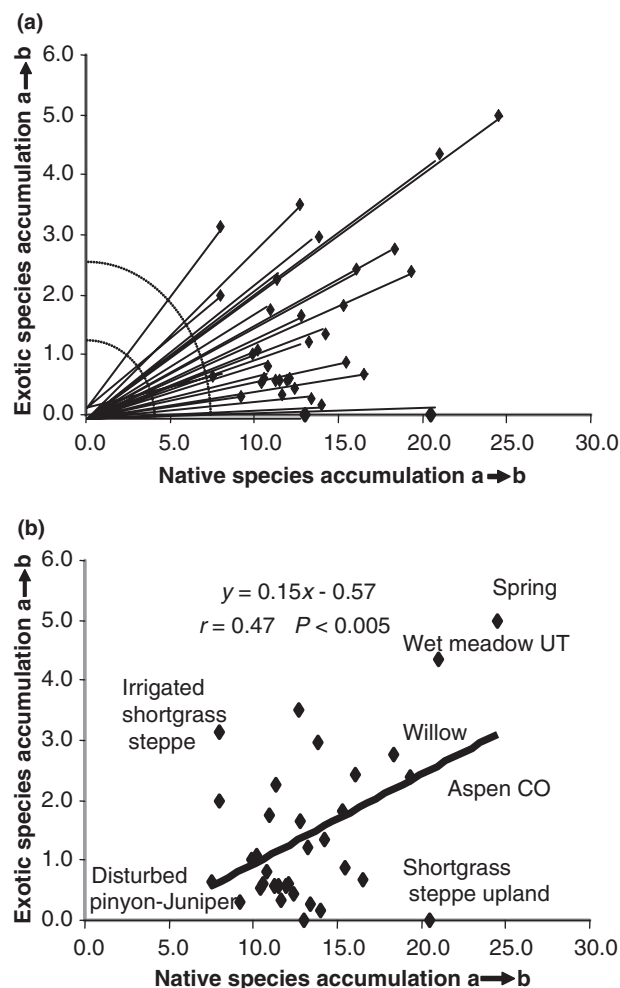
2006b). In 36 vegetation types (assumed to be typical plant assemblages or communities in natural areas), we established a large 20 m × 50 m (1000 m<sup>2</sup>) plot containing one 100-m<sup>2</sup> subplot (5 m × 20 m) in the center, two 10-m<sup>2</sup> subplots, and 10 1-m<sup>2</sup> subplots. It was instructive to find that non-native plant species typically represent about 10.5% of the flora in 1-m<sup>2</sup> subplots, and about 9.8% of the total vegetation cover across the vegetation types. At the 1000-m<sup>2</sup> scale, non-native species typically represented < 8% of the total flora in the same vegetation types, suggesting that native species accumulate with area faster than non-native species at the same types (Stohlgren *et al.* 2006b). Non-native plant species only achieved substantial cover, but still < 50%, in irrigated short-grass steppe pastures and disturbed (burned) pinyon-juniper stands (see Stohlgren *et al.* 2006b for more details).

We focused on the 100-m<sup>2</sup> subplot and 1000-m<sup>2</sup> plot data to examine species accumulation rates of native and non-native species at plot scales because the smaller subplots could be affected by the size of individuals (i.e. trees vs. grasses and herbs; physical limitation causing very local saturation; Loreau 2000) and extremely high variation in plant species composition (Stohlgren *et al.* 2006b). Cumulative native and exotic plant species presence was recorded in nested 100- and 1000-m<sup>2</sup> plots (5 × 20 m and 20 × 50 m plots; Stohlgren *et al.* 2005b, 2006b). In addition, an index of both native and exotic plant species at the 'landscape-scale' were developed from cumulative species curves (Gotelli & Colwell 2001) from five randomly selected, widely scattered 1000-m<sup>2</sup> plots in a vegetation type to assess the relationship

of landscape-scale richness to the 'local-scale' (plot-scale) accumulation in native and exotic species between 100- and 1000-m<sup>2</sup>.

We hypothesized that all vegetation types would accumulate native plant species between the 100- and 1000-m<sup>2</sup> plots (i.e. even modest spatial scales) due to increased area and heterogeneity (Arrhenius 1921; Sax 2002; Stohlgren *et al.* 2006b). Additionally, some communities would accumulate (in space) exotic species at a faster rate than others (Gilbert & Lechowicz 2005), perhaps positively affected by the size of the exotic regional species pool. If the general trend in several vegetation types was positive in both native and exotic species accumulations, this relationship may provide a possible explanation for the temporal patterns of plant invasion (this paper), and the spatial patterns of plant invasion in the USA (Stohlgren *et al.* 2003, 2005a). We also hypothesized that the size of the regional species pool of native and exotic plant species would be positively associated with the rate of 'local-scale' (plot-scale) accumulation in native and exotic plant species.

We found considerable native and exotic plant species accumulation between 100-m<sup>2</sup> and 1000-m<sup>2</sup> plots in most of the 36 vegetation types studied (Fig. 5a). We also found a significant positive relationship between native species accumulation and exotic species accumulation between 100-m<sup>2</sup> and 1000-m<sup>2</sup> plots across the 36 vegetation types (Fig. 5b). The types of communities that accumulated the greatest numbers of native and exotic species included springs, wet meadows and aspen (*Populus tremuloides*) types that are generally high in water, light and soil nitrogen;



**Figure 5** (a) Observed accumulation of native and exotic species over modest spatial scales (from 100 m<sup>2</sup> to 1000 m<sup>2</sup>) for 36 vegetation types in the central US. (b) The relationship of native and exotic species accumulation (i.e. gained between 100-m<sup>2</sup> (a) and 1000-m<sup>2</sup> (b) plots for 36 vegetation types in the central US (adapted from data in Stohlgren *et al.* 2006b).

conditions optimal for productivity and diversity (Stohlgren *et al.* 2006b). These communities are likely not saturated at these spatial scales. The types of communities that accumulated the fewest native and exotic species with increased area included disturbed pinyon-pine and xeric communities in southern Utah, where water stress is evident (Stohlgren *et al.* 2006b). Heavily disturbed areas, such as irrigated shortgrass steppe, accumulated a relatively high numbers of exotic species with increases in area, while some community types (e.g. tundra [13 x, 0 y] and upland shortgrass steppe) accumulated almost no additional exotic species between 100-m<sup>2</sup> and 1000-m<sup>2</sup> plot scales. However, both scales did contain some generalist invaders such as dandelion (*Taraxacum* spp.) or cheatgrass (*Bromus tectorum*).

Habitat heterogeneity may be an important contributor to the observed patterns, further promoting coexistence. We had several measures of habitat heterogeneity and species richness for 79 plots (of the 727 plots used above) in Colorado (Kumar *et al.* 2006). These data show that at both plot-level spatial scales (100 m<sup>2</sup> and 1000 m<sup>2</sup>), models using native species richness or habitat heterogeneity alone perform significantly less well than when combined, and that the effect (standardized partial regression coefficient) of habitat heterogeneity is greater than the effect of native species richness (Table 3). We propose that spatial heterogeneity increases with scale, from within plot scales of 100 m<sup>2</sup> and 1000 m<sup>2</sup> to landscape, regional and national scales (Table 3).

## SYNTHESIS

### No sign of plant species saturation from local to national scales

The spatial patterns of native and exotic species accumulation (i.e. species-area relationships) may provide important insights into the mechanisms of plant invasions in space and time. It follows that the lack of plant species saturation at local scales may produce similar patterns at regional and

**Table 3** Effects of native species richness (at 100 m<sup>2</sup> and 1000 m<sup>2</sup>) and habitat heterogeneity (in a 240-m radius around the plots) as predictors of non-native species richness (at 100 m<sup>2</sup> and 1000 m<sup>2</sup>) in 79 0.1 ha plots in Rocky Mountain National Park, Colorado, USA

Dependent variable	Predictor(s)	$\beta$	$F$	d.f.	Adj. $r^2$	AICc
Non-native species (100 m <sup>2</sup> )	Native species richness alone	0.35	10.83	1, 77	0.11	9.49
	Habitat heterogeneity alone	0.41	15.81	1, 77	0.16	5.14
	Native species richness plus	0.27	12.04	2, 76	0.22	0.37
	Habitat heterogeneity	0.35				
Non-native species (1000 m <sup>2</sup> )	Native species richness alone	0.56	36.12	1, 77	0.31	28.65
	Habitat heterogeneity alone	0.43	17.14	1, 77	0.17	43.16
	Native species richness plus	0.30	25.37	2, 76	0.38	20.86
	Habitat heterogeneity	0.48				

All models significant at  $P < 0.0001$ . Habitat heterogeneity is represented as Simpson's index of vegetation patch diversity in a 240-m radius of the each plot (see Kumar *et al.* 2006 for details). All factors were log<sub>10</sub> transformed.



national scales. First, native species accumulation in space is impressive even between 100-m<sup>2</sup> and 1000-m<sup>2</sup> plots for most vegetation types studied to date (Fig. 4; Keeley *et al.* 2003). Furthermore, most studies of species-accumulation or species–area relationships fail to find a true leveling off or asymptote, because additional environmental gradients are continually crossed with increasing area. Thus, there is little theoretical reason for native species saturation in most vegetation types. The positive trend in both native and exotic species suggests that turnover rates may be higher in species rich communities. If we found no relationship between native species accumulation and exotic species accumulation, it may have suggested elements of biotic resistance or competitive exclusion, or that non-native species do not respond to scale or heterogeneity in the same way native species respond. A more plausible explanation is that turnover increases with scale and heterogeneity (Table 3), native and non-native species behave similarly, and the turnover rate may be faster in species-rich vegetation types, but that exotic species currently represent a small fraction of the richness and cover at any sites. This results in species coexistence despite increasing invasion (at least for now).

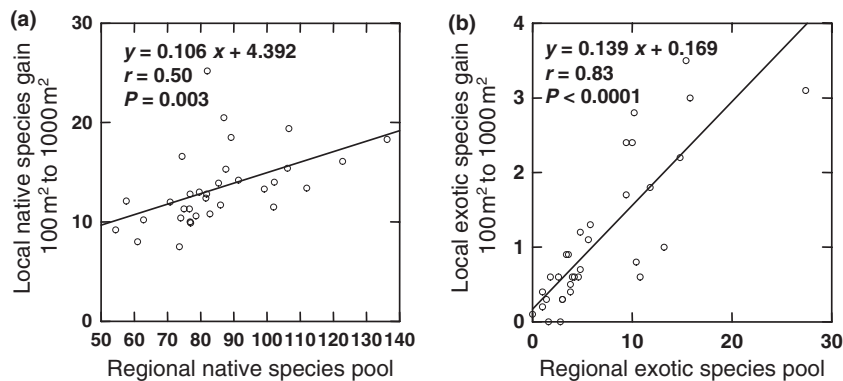
Second, we found a significant positive association between the size of the regional native plant species pool and the rate of native species accumulation at the local-scale between 100 m<sup>2</sup> and 1000 m<sup>2</sup> (Fig. 6a). We found an even stronger relationship between the regional-scale exotic plant species pool and the rate of exotic species accumulation at the local-scale (Fig. 6a). It follows that increases in the regional pool of exotic plant species (Fig. 6b) might result in increased establishment at local scales (Fig. 5b), but this will take detailed monitoring to confirm. Still, there may be a positive feedback loop, between external propagule presence or pressure (from seeds outside the plots, but in the community), and local species establishment, turnover, and accumulation at plot scales (Valone & Hoffman 2002). Newly arriving immigrants from the landscape species pool might increase local propagule pressure, and further the

establishment and spread of exotic species in a vegetation type. Thus, over time, we might see a closer link between  $\alpha$ ,  $\beta$  and  $\gamma$  diversity at local and regional scales (Loreau 2000), and especially for easily dispersed exotic species.

Third, patterns of plant invasions in space (Figs 5 and 6b, Stohlgren *et al.* 2005a), and time (Figs 1–3), clearly show that species-rich areas, despite the theories of competitive exclusion and species saturation, continue to be invaded at greater rates than species-poor areas (Figs 3 and 5b, Fridley *et al.* 2007). It is tempting to view our plot-based research as the interim result of 400 years of invasion by exotic species, but differences in dispersal, time since invasion, and proximity to past invasions (Pyšek & Hulme 2005) make it difficult to draw temporal conclusions from this snapshot in time. Nevertheless, the patterns observed in Figs 5 and 6 would provide the most parsimonious explanation for the patterns shown in Fig. 3; namely that species rich communities are more prone to invasion than species-poor types and that the accumulation of native and exotic species reflects similar responses to environmental conditions (Fig. 5b). Thus, the escalating diversity of native and exotic species in an area is dependent on available light, water, soil nutrients, warm temperatures, and habitat heterogeneity provided by microsites, small and large-scale disturbances, species turnover, and species pools (Table 3, Hillebrand 2005; Ricklefs 2006; Stohlgren *et al.* 2006b).

We propose that species turnover in space and time are interrelated. Just as environmental gradients, habitat heterogeneity, and regional species pools increase with area and promote species turnover in space, the number of plants that die and the area disturbed, which also increase in space, may promote species turnover in time. This predisposes and accelerates invasion where non-native propagules are present in the regional species pool (Figs 5 and 6). In this way, a continued influx of non-native propagules from trade, transportation, or long range dispersal results in accumulations of naturalized non-native species. Extirpation of native species caused by non-native plant species is difficult to demonstrate at the scales of plant

**Figure 6** (a) Relationships of regional native species pool (species richness in five widely distributed 1000-m<sup>2</sup> plots in a vegetation type) and 'local' (plot-scale) native species accumulation between 100-m<sup>2</sup> and 1000-m<sup>2</sup> plots for 32 vegetation types in the central US. (b) Same as above for exotic species. Vegetation types with < 5 plots were excluded from this analysis.



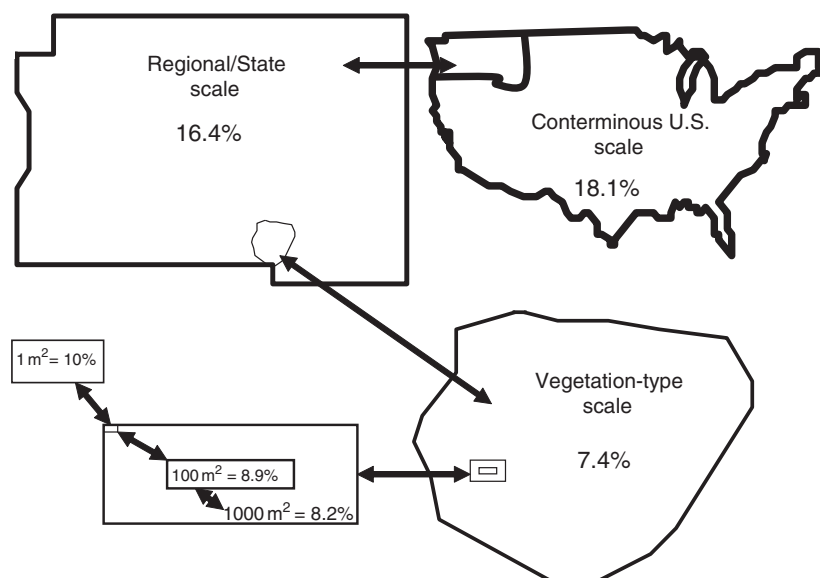
communities, counties, areas larger than a few hectares, or even at the plot scales we measure. Despite invasions, species coexistence is observed even at modest spatial scales. Thus, species turnover in space is expected to be correlated with invasion over time (Fig. 5; Davis *et al.* 2005; Stohlgren *et al.* 2006b).

Our main conclusion is that there is little evidence of plant species saturation at plots scales ( $> 100 \text{ m}^2$ ), plant assemblage or community scales (Figs 5 and 6), county or regional scales (Figs 1–3, Stohlgren *et al.* 2005a), or state or national scales (Table 1). We recognize that the concept of ‘community saturation’ is composed of two ambiguous terms. A ‘community’ is generally defined as a group of species that regularly occur together in similar environments. However, communities are difficult to delineate, ecotones can be broad, and most environments change in time and space; there is often high overlap of species among communities; low interactions among many rare species and high species turnover in space and time within and among communities; and there are high rates of invasion in many communities (Rosenzweig 1995; Ricklefs 2006; Stohlgren 2007). Furthermore, saturation is affected by the spatial and temporal scale of observations (Stohlgren *et al.* 2006b, Fridley *et al.* 2007), the adaptations of species for coexistence, and changing species–environment relationships. Thus, species saturation may be a moving target as the extent of the study area is increased or over time. At present, on average, non-native plant species make up, on average, only about 10–20% of the floras at each scale (Fig. 7).

However, it should be clear that it is unreasonable to expect competitive exclusion (*sensu* Tilman 1999; Kennedy *et al.* 2002) to be a major force inhibiting future immigration and invasions. It also seems unlikely, given the first

400 years of colonization by exotic species in the US that other biotic resistance mechanisms (e.g. herbivory, pathogens) will be fully effective in inhibiting the establishment, reproduction and spread of invasive plants species. Ecologists need to focus on the rates of exotic species colonization, growth, spread and effects in space and time. In regards to exotic species patterns in space, we have generally found that: (i) large resource-rich, open, warm, wet areas generally accommodate more exotic species than resource poor, cold, stressed areas, and that area alone is a poor predictor of species richness; (ii) strong positive relationships exist between exotic species richness and native richness or total cover or biomass; and (iii) heterogeneous areas generally accommodate more exotic species than homogeneous areas (Stohlgren *et al.* 2005a; Kumar *et al.* 2006).

With respect to time, we believe that exotic species are probably accumulating due to their effective means of reproduction, continued introduction and spread (Figs 1c, 2 and 3). Because extirpation and extinction of native species is a much slower process than immigration and colonization (Table 1), and because of the positive relationships between local ( $\alpha$ ) and regional ( $\gamma$ ) diversity (Fig. 6), we can expect continued coexistence of native and exotic plant species at large spatial scales (Levine 2000). However, as witnessed by the invasion of *Tamarix* sp., *Spartina* sp., *Phragmites* sp., and *Euphorbia esula*, we are concerned that the inevitable introduction of major biomass producing, dominating or noxious exotic species may drastically alter local native species populations, composition, habitat quality and ecosystem services. Thus, it is inevitable that some local replacement of native species by a limited number of extremely invasive exotics



**Figure 7** Schematic of the average contribution of non-native plant species to the total species pool at various spatial scales from available data.



will occur, thus resulting in local extirpations. However, the most general broad-scale pattern is one of invasion and coexistence.

Similar 'rich-get-richer' patterns are being reported around the globe as witnessed in the Czech Republic (Chytrý *et al.* 2005), Great Britain (Maskell *et al.* 2006), and Mediterranean region (Vila *et al.* 2007). Immigrations (invasions) are vastly outpacing extinctions. It is too early to say if we are building up an 'extinction deficit' (Vellend *et al.* 2006; but see Adriaens *et al.* 2006) or simply contributing to long-term coexistence. Managers of natural areas should assume an environment of increasing invasions and continued coexistence. Increased trade and travel will likely continue to bring many new invaders to the US. We need a greater emphasis on early detection and rapid response, and better monitoring of invaders from multiple biological groups. We need to share data faster to create living maps and predictive models of harmful species.

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## REFERENCES

- Adriaens, D., Honnay, O. & Hermy, M. (2006). No evidence of a plant extinction debt in highly fragmented calcareous grasslands in Belgium. *Biol. Cons.*, 133, 212–224.
- Arrhenius, O. (1921). Species and area. *J. Ecology*, 9, 95–99.
- Chytrý, M., Pyšek, P., Tichý, L., Knollová, I. & Danihelka, J. (2005). Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. *Preslia*, 77, 339–354.
- Davis, M.A., Thompson, K. & Grime, J.P. (2005). Invasibility: the local mechanism driving community assembly and species diversity. *Ecography*, 28, 696–704.
- Elton, C.S. (1958). *The ecology of invasions by animals and plants*. Methuen, London.
- Flather, C., Stohlgren, T.J., Barnett, D., Jarnevich, C. & Kartesz, J. (2006). Plant species invasions along the latitudinal gradient in the United States: a reply to Fridley *et al.* *Ecology*, 87, 3213–3217.
- Freestone, A.L. & Harrison, S. (2006). Regional enrichment of local assemblages is robust to variation in local productivity, abiotic gradients, and heterogeneity. *Ecol. Lett.*, 9, 95–102.
- Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D. *et al.* (2007). The invasion paradox: reconciling pattern and process in species invasions. *Ecology*, 88, 1–17.
- Gilbert, B. & Lechowicz, M.J. (2005). Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. *Ecology*, 86, 1848–1855.
- Gotelli, N.J. & Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.*, 4, 379–391.
- Grime, J.P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, 242, 344–347.
- Hillebrand, H. (2005). Regressions of local on regional diversity do not reflect the importance of local interactions or saturation of local diversity. *Oikos*, 110, 195–198.
- Huston, M.A. (1979). A general hypothesis of species diversity. *Am. Nat.*, 113, 81–101.
- Kartesz, J.K. (2008). Floristic synthesis of North America. *Biota of North America Program*. Digital Database. Chapel Hill, NC (In Press).
- Keeley, J.E., Lubin, D. & Fotheringham, C.J. (2003). Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecol. Appl.*, 13, 1355–1374.
- Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P. (2002). Biodiversity as a barrier to ecological invasion. *Nature*, 417, 636–638.
- Kumar, S., Stohlgren, T.J. & Chong, G.W. (2006). Effects of spatial heterogeneity on native and non-native plant species richness. *Ecology*, 87, 3186–3199.
- Levine, J.M. (2000). Species diversity and biological invasions: relating local process to community pattern. *Science*, 288, 852–854.
- Lonsdale, W.M. (1999). Global patterns of invasions and the concept of invasibility. *Ecology*, 80, 1522–1536.
- Loreau, M. (2000). Are communities saturated? On the relationship between  $\alpha$ ,  $\beta$  and  $\gamma$  diversity. *Ecol. Lett.*, 3, 73–76.
- MacArthur, R.H. & Wilson, E.O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, 17, 373–387.
- Mack, R.N., Simberloff, D., Lonsdale, M., Evans, H., Clout, M. & Bazzaz, F. (2000). Biotic invasions: causes, epidemiology, global consequences and control. *Issues Ecol.*, 5, 1–20.
- Maskell, L.C., Firbank, L.G., Thompson, K., Bullock, J.M. & Smart, S.M. (2006). Interactions between non-native plant species and the floristic composition of common habitats. *J. Ecology*, 94, 1052–1060.
- Palmer, M.W. (2005). Temporal trends of exotic species richness in North American floras: an overview. *Ecoscience*, 12, 386–390.
- Palmer, M.W. (2006). Scale dependence of native and alien species richness in North American floras. *Preslia*, 78, 427–436.
- Pyšek, P. & Hulme, P.E. (2005). Spatio-temporal dynamics of plant invasions: linking pattern to process. *Ecoscience*, 12, 302–315.
- Pyšek, P., Sádlo, J. & Mandák, B. (2003). Czech alien flora and the historical pattern of its formation: what came first to central Europe? *Oecologia*, 135, 122–130.

- Rejmánek, M. (1996). Species richness and resistance to invasions. In: *Biodiversity and ecosystem processes in tropical forests*, *Ecological Studies* 122 (eds Oriens, H., Dirzo, R. & Cushman, J.H.). Springer-Verlag, Berlin, pp. 153–172.
- Richardson, D.M., Rouget, M., Ralston, S.J., Cowling, R.M., Van Rensburg, B.J. & Thuiller, W. (2005). Species richness of alien plants in South Africa: environmental correlates and the relationship with indigenous plant species richness. *Ecoscience*, 12, 391–205.
- Ricklefs, R.E. (2006). Evolutionary diversification and the origin of the diversity–environment relationship. *Ecology*, 87, S3–S13.
- Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Sax, D.F. (2002). Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Divers. Distrib.*, 8, 193–210.
- Stohlgren, T.J. (2007). *Measuring Plant Diversity: Lessons from the Field*. Oxford University Press, New York, 390 pp.
- Stohlgren, T.J., Barnett, D.T. & Kartesz, J. (2003). The rich get richer: patterns of plant invasions in the United States. *Front. Ecol. Environ.*, 1, 11–14.
- Stohlgren, T.J., Barnett, D.T., Flather, C., Kartesz, J. & Peterjohn, B. (2005a). Plant species invasions along the latitudinal gradient in the United States. *Ecology* 86, 2298–2309.
- Stohlgren, T.J., Guenther, D.A., Evangelista, P.H. & Alley, N. (2005b). Patterns of plant species richness, rarity, endemism, and uniqueness in an arid landscape. *Ecol. Apps*, 15, 715–725.
- Stohlgren, T.J., Barnett, D., Flather, C., Fuller, P., Peterjohn, B., Kartesz, J. *et al.* (2006a). Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biol. Invasions*, 8, 427–447.
- Stohlgren, T.J., Jarnevich, C.S., Chong, G. & Evangelista, P. (2006b). Scale and plant invasions: a theory of biotic acceptance. *Preslia*, 78, 405–426.
- Tilman, D. (1999). The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, 80, 1455–1475.
- Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences, USA*, 101, 10854–10861.
- Valone, T.J. & Hoffman, C.D. (2002). Effects of regional pool size on local diversity in small-scale annual plant communities. *Ecol. Lett.*, 5, 477–480.
- Vellend, M., Verheyen, K., Jacquemyn, Kolb, A., Van Calster, H., Peterken, G. *et al.* (2006). Extinction debt of forest plants persist for more than a century following habitat fragmentation. *Ecology*, 87, 542–548.
- Vila, M., Pino, J. & Font, X. (2007). Regional assessment of plant invasions across different habitat types. *J. Vegetation Science*, 18, 35–42.

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## COMMENTARY ON STOHLGREN *ET AL.* (2008): THE MYTH OF PLANT SPECIES SATURATION

Stohlgren *et al.* have performed the field a tremendous service by leading us to think about diversity, invasibility, and community saturation across large geographic scales. In this paper, they make a strong case for the striking conclusion that at county to state scales, exotic plant invasions have led to few native plant extinctions. However, I think the more general question of whether communities are ever closed to immigration should still be regarded as open.

## SPACE-FOR-TIME SUBSTITUTIONS MUST BE USED CAUTIOUSLY

The ideal way to test for saturation would be to determine whether rates of colonization and extinction depend on species richness, using either long-term observations or manipulations of richness in natural communities. Such data are too scarce to permit any final conclusions about the prevalence of saturation. The authors do have good

observational data at the county to state scale, showing that exotic richness has continued to increase over time, and that the positive spatial correlation between native and exotic richness has strengthened. This demonstrates that competitive exclusion of natives by exotics is absent or weak at that scale compared with other influences on species richness.

At the local community scale, in the absence of either temporal or experimental data, a common approach has been to ask how native and exotic species richness are correlated in space. This correlation is sometimes positive, at least at moderately large scales, indicating that native and exotic richness respond similarly to environmental gradients (e.g. Lonsdale 1999; Stohlgren *et al.* 1999; Levine 2000; Davies *et al.* 2005). Whether this really indicates a lack of saturation, in the sense that native and exotic richness have no effect on one another, is considered below.

In this paper, the authors use a different space-for-time tactic to demonstrate unsaturation. Using nested plots, they show that both native and exotic richness increase substantially from the 100 m<sup>2</sup> to the 1000 m<sup>2</sup> scale, and that the strength of this species-area increase is correlated